Feeding interactions between native freshwater mussels (Bivalvia: Unionidae) and zebra mussels *(Dreissena polymorpha)* in the Ohio River

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Abstract: The effects of zebra mussel infestation on the feeding of native unionids in the Ohio River were evaluated through gut contents and available food in the water column. In 1996, heavily infested *Amblema plicata* (Say, 1817) and *Quadrula pustulosa* (I. Lea, 1831) had significantly less ($p < 0.01$) organic matter in their guts (1.4 and 0.6 mg ash-free dry weight [AFDW], respectively) than lightly infested specimens (4.6 and 1.8 mg AFDW, respectively), and heavily infested *Q. pustulosa* had a significantly lower ($p < 0.05$) mean algal cell number (1.8×10^4) in the guts than lightly infested specimens (3.9×10^5). However, mean algal cell numbers in the guts of heavily infested and lightly infested *A. plicata* (5.7×10^5 versus 9.1×10^5, respectively) were not significantly different ($p = 0.17$). In 1997, significant reductions ($p < 0.05$) in total algal cells and organic matter in gut samples again occurred for heavily versus lightly infested individuals of both species. In addition, gut contents of individual *A. plicata* from one of two sites contained significantly less ($p < 0.05$) organic matter (0.92 versus 4.55 mg AFDW) and fewer algal cells (9.4×10^4 versus 2.3×10^5) than the combined gut contents of all zebra mussels (18-33 mm in length) attached to their shells. Gut analyses also revealed significant diet overlap between native unionids and infesting zebra mussels. Water samples collected from just above the mussel beds in 1997 showed that algal densities and total suspended solids at the heavily infested site (> 360 zebra mussels/m^2) were reduced by more than 50%, when compared to samples collected from the surface. Thus, competitive interactions or interference by zebra mussels likely reduced the availability of algal and detrital food resources for consumption by unionids.

Key words: algae, zebra mussels, unionids, Ohio River, competition

Since its introduction into Lake St. Clair, the zebra mussel, *Dreissena polymorpha* (Pallas, 1771), has greatly reduced phytoplankton and bacterioplankton levels in the Great Lakes (Wu and Culver, 1991; MacIsaac *et al.*, 1992; Cotner *et al.*, 1995; Fanslow *et al.*, 1995; Heath *et al.*, 1995). Phytoplankton levels in Lake Erie, for example, dropped 62-92% (Leach, 1993), and planktonic diatoms decreased 85% despite sufficient nutrients for growth (Holland, 1993). Consequently, Secchi disk transparencies in Lake Erie have increased 85% (Leach, 1993). Phytoplankton grazing by zebra mussels also can alter the composition of the phytoplankton community. In Lake Huron, for example, zebra mussel feeding has shifted dominance from diatoms to filamentous green algae (Lowe and Pillsbury, 1995), and recent studies show selective rejection of the nuisance bluegreen alga *Microcystis* by zebra mussels, such that *Microcystis* becomes dominant in the plankton (H. Vanderploeg, NOAA, pers. comm.)

Zebra mussel colonization of the Great Lakes also has caused dramatic declines in the survival and fitness of native freshwater mussel populations (Hebert *et al.*, 1991; Hunter and Bailey, 1992; Haag *et al.*, 1993; Gillis and Mackie, 1994; Nalepa, 1994; Schloesser and Nalepa, 1994). By attaching to the shells of unionids, zebra mussels can directly affect unionid survival by interfering with feeding, respiration, balance, burrowing, and locomotion (Mackie, 1991; reviewed by Schloesser *et al.*, 1996). Large densities of zebra mussels, however, also can affect unionid survival indirectly by reducing or removing food resources from the water column (Lewandowski, 1976; Hebert *et al.*, 1991; Mackie, 1991; Haag *et al.*, 1993). A large gill-area to body-dry-weight ratio, and a large number of gill cirri in individual zebra mussels, allow for increased filtration efficiency and filtration rate relative to those of native unionids (Silverman *et al.*, 1995). Filtration rates of the freshwater mussel, *Lampsilis siliquoidea* (Barnes, 1823), for example, were found to be only one-tenth the filtration rate of individual zebra mussels (Heath *et al.*, 1995). In laboratory experiments, Baker and Hornbach (1997) reported that *Amblema plicata* (Say, 1817) filtered 74 ml/hr, while the 28 infesting zebra mussels filtered 130 ml/hr as a group. Thus, relatively small populations of zebra mussels can affect the feeding of unionids.

Zebra mussel populations in the lower Ohio River have achieved densities comparable to those in the Great Lakes (350,000/m²; A. Miller, USACOE, pers. comm.). Because of documented impacts to the phytoplankton communities and native mussel populations of the Great Lakes, large populations of zebra mussels in the Ohio River could have similar consequences for native mussel populations. Strayer and Smith (1996) found that low zebra mussel infestation rates in the Hudson River were associated with high unionid mortality and hypothesized that reduced food resources might be the cause. No studies, however, have directly confirmed whether zebra mussels affect the feeding of unionids in a riverine environment where organic materials are continually supplied from upstream. Thus, the objective of this study was to determine whether zebra mussels reduce unionid ingestion of phytoplankton and organic matter by (1) ingesting similar food resources, and (2) reducing food resources at the sediment-water interface.

METHODOLOGY

On 23 July 1996, ten specimens each of the threeridge, *Amblema plicata*, and the pimpleback, *Quadrula pustulosa* (I. Lea, 1831), were collected from a lightly infested site on the Ohio River near Parkersburg, West Virginia, which had a mean density of 0.3 zebra mussels/m², and a maximum of one zebra mussel/unionid (P. Morrison, USFWS, pers. comm.). On 16 August 1996, ten specimens of *A. plicata* were collected from a heavily infested site near Paducah, Kentucky, which had 3,600 zebra mussels/m² (A. Miller, USACOE, pers. comm.). Specimens of *Q. pustulosa* were difficult to find at this site, so on 21 August 1996, ten specimens were collected from another heavily infested site near Maysville, Kentucky, which had 360 zebra mussels/m² and a maximum of 92 zebra mussels/unionid (P. Morrison, USFWS, pers. comm.). In the field, mussel bodies were removed from shells, weighed, preserved in 95% ethanol, and transported to the laboratory for analysis.

In 1997, ten specimens each of *A. plicata* and *Q. pustulosa* were collected from a highly infested (370 zebra mussels/m²) and a lightly infested (< 1 zebra mussel/m²) site on the Ohio River for gut content analysis. In addition, all zebra mussels, 18-33 mm in length, attached to the shells of *A. plicata* were removed and preserved in 95% ethanol for gut content analysis. Zebra mussels 18-33 mm in length were chosen, because it is difficult to remove the entire gut contents of smaller individuals. At each collection site, water samples with algae were collected from the the surface and overlying the mussel bed, fixed with acid Lugol's solution (Saraceni and Ruggiu, 1969), and placed in settling chambers to compare the density and relative abundance of algal genera using inverted microscopes. Aliquots of 100 ml were then filtered through pre-ashed Whatman GF/F filters, dried (100°C), and ashed (500°C) to determine the ash-free dry weight (AFDW) of seston.

Gut contents of unionids and of zebra mussels attached to *Amblema plicata* were individually removed from each specimen, pooled, then suspended in 3 ml of water, and fixed with 50 µl of acid Lugol's solution for analysis. A 50 µl aliquot of the gut contents was placed on a microscope slide. Ocular grids divided the field of view into 59 transects, and algal cells were counted and identified to genus from two transects using an Ausjena/Nomarsky microscope at 400X. The variability of this semi-quantitative method (± 20%, $\alpha = 0.05$) was determined using ten counts from the same sample. The remaining gut contents were collected on pre-ashed Whatman GF/F filters, dried (100°C), and ashed in a muffle furnace (500°C) overnight to determine AFDW. Mean algal cell numbers and mean AFDW values in the gut samples of each species were compared by ANOVA.

RESULTS

In 1996, significant differences in total algal cells and organic matter were observed in guts of lightly and heavily infested unionids (Table 1). While mean algal cell numbers in guts of lightly and heavily infested *Amblema plicata* (5.7×10^5 versus 9.1×10^5 cells) were not significantly different ($p = 0.17$), the gut contents of lightly infested *A. plicata* had significantly more ($p < 0.01$) organic matter (4.6 mg AFDW) than heavily infested specimens (1.4 mg AFDW). Heavily infested *Quadrula pustulosa* showed significantly lower ($p < 0.05$) organic matter and mean algal cell number (0.6 mg AFDW and 1.8×10^4 cells, respectively) than lightly infested specimens (1.8 mg AFDW and 3.9×10^5 cells, respectively).

In 1997, significant reductions in organic matter content and total algal cells also were observed in guts of heavily infested unionids (Table 2). Organic matter content and total algal cells were significantly lower ($p < 0.05$) in the guts of heavily infested *Amblema plicata* (0.9 mg

Table 1. Mean algal cell number and ash-free dry weight (AFDW; ± SD) in guts of *Amblema plicata* and *Quadrula pustulosa* heavily infested (H) and lightly infested (L) with zebra mussels, July-August 1996.

Species	N	Algal Cell Number	AFDW (mg)
A. plicata (L)	11	$9.1 \times 10^5 \pm 6.0 \times 10^5$	4.6 ± 0.9
A. plicata (H)	10	$5.7 \times 10^5 \pm 4.9 \times 10^5$	1.4 ± 0.7
Q. pustulosa (L)	10	$3.9 \times 10^5 \pm 2.8 \times 10^5$	1.8 ± 1.0
Q. pustulosa (H)	10	$1.8 \times 10^4 \pm 9.2 \times 10^3$	0.6 ± 0.3

Table 2. Mean algal cell number and ash-free dry weight (AFDW; ± SD) in guts of *Dreissena polymorpha* and of *Amblema plicata* and *Quadrula pustulosa* heavily infested (H) and lightly infested (L) with zebra mussels, July-August 1997.

Species	N	Algal Cell Number	AFDW (mg)
A. plicata (L)	10	$5.5 \times 10^6 \pm 2.4 \times 10^6$	5.1 ± 1.7
A. plicata (H)	10	$9.4 \times 10^4 \pm 7.6 \times 10^4$	0.9 ± 0.8
Q. pustulosa (L)	10	$1.9 \times 10^6 \pm 1.3 \times 10^6$	2.0 ± 1.2
Q. pustulosa (H)	9	$6.9 \times 10^4 \pm 7.3 \times 10^4$	0.3 ± 0.2
D. polymorpha	9	$2.3 \times 10^5 \pm 1.3 \times 10^5$	4.6 ± 3.6

AFDW and 9.4×10^4 cells, respectively) than lightly infested specimens (5.1 mg AFDW and 5.5×10^6 cells, respectively). Significant reductions in both organic matter content and total algal cells also were observed for heavily infested (0.3 mg AFDW and 6.9×10^4 cells, respectively) versus lightly infested (2.0 mg AFDW and 1.9×10^6 cells, respectively) *Quadrula pustulosa*.

Examination of unionid guts in 1996 and 1997 indicated that *Amblema plicata* and *Quadrula pustulosa* readily ingested a significant amount of detritus (ca. 90%) along with algal cells between 4 and 80 µm in length. Diatoms (Bacillariophyta) and green algae (Chlorophyta) dominated gut samples, and the dominant algal genera in 1996 (*Chlorella, Cyclotella, Navicula, Melosira*, and *Scenedesmus*; Table 3) and 1997 (*Chlorella, Cyclotella, Mougeotia, Melosira*, and *Scenedesmus*; Table 4) were similar. Usually, the relative abundance of algal genera within unionid guts was very similar to relative abundances of algae in water samples collected from the river bottom (Table 5). Interestingly, the pennate diatom *Synedra* dominated water samples at the lightly infested site (43%), but few if any of these > 100 µm-long cells were found in the unionid guts. In 1997, algal cell densities and seston AFDW at the water surface (8.37×10^4 cells/ml and 9.0 mg/l, respectively) and above the mussel bed (8.42×10^4 cells/ml and 9.0 mg/l, respectively) were nearly identical at the lightly infested site (Table 5). Seston AFDW (5.0 mg/l) and algal cell densities (2.2×10^4 cells/ml) overlying the mussel bed at the heavily infested site, however, were greatly reduced compared to samples taken from the surface (7.2 mg/l and 8.3×10^4 cells/ml, respectively).

In 1997, individual *Amblema plicata* collected from the heavily infested site were infested with > 100 zebra mussels/unionid, averaging 50 zebra mussels between 18 and 33 mm in length. Gut contents of zebra mussels contained large amounts of detritus. Pooled samples of zebra mussel guts contained five times more ($p < 0.05$) organic matter (4.55 mg versus 0.92 mg, respectively) and twice as many algal cells (2.3×10^5 cells versus 9.4×10^4 cells, respectively) than the specimen of *A. plicata* to which they were attached (Table 3). In addition, the dominant algal genera – *Chlorella, Cyclotella, Mougeotia, Melosira*, and *Scenedesmus* – and range of cell sizes (4-70 µm) in zebra mussel guts were nearly identical to those in infested *A. plicata* (Table 4). Relative abundances of algal genera within zebra mussel guts were similar to relative abundances in water samples collected from the river bottom (Table 5).

DISCUSSION

Reduced food resources at the sediment-water interface can cause decreased growth rates in bivalves despite adequate food resources at the water surface (Frechette and Bourget, 1985). This phenomenon could be particularly important for unionids in the lower Ohio River because zebra mussels occur in large densities at the sediment-water interface and often attach directly to the shells of unionids. In fact, water samples collected from just above the mussel beds in 1997 showed that algal densities and AFDW at the heavily infested site (> 360 zebra mussels/m^2) were reduced by more than 50% when compared to samples collected from the surface. Thus, it appears that zebra mussel densities in heavily infested sections of the Ohio River contribute to reduced food resources at the sediment-water interface.

Regardless of reductions in total algal cell densities, the effects of zebra mussel infestation on unionid ingestion can be reduced if zebra mussels and unionids selectively feed on different food types. Currently, studies on selective feeding in bivalves appear to be inconclusive. Some authors have concluded that bivalves select food particles of high quality (Allen, 1914; Loosanoff and Engel, 1947; Shumway *et al.*, 1985), while others have concluded that feeding is non-selective (Churchill and Lewis, 1924; Gale and Lowe, 1971; Bayne *et al.*, 1976). Thus, selective feeding could be species dependent. Zebra mussels have been reported to ingest a wide range of food particles between 0.7 and 450 µm (Mikheyev, 1967; Jorgensen *et al.*, 1984). However, Sprung and Rose (1988) indicated that retention efficiency in zebra mussels is maximized for food particles between 5-35 µm; Ten Winkle and Davids (1982) also concluded from gut content analysis that zebra mussels select particles between 15-50 µm. In our study, zebra mussel gut samples contained food particles between 4-70 µm in maximum dimension. In comparison, Miura and Yamashiro (1990) indicated that the unionid *Anodonta calipygos* (Kobelt, 1879) ingests food particles between 0.5 and 100 µm. Like for the zebra mussel, maximum retention efficiencies were

Table 3. Percent relative abundances (SD) of algae in guts of lightly (L) and heavily (H) infested *Amblema plicata* and *Quadrula pustulosa* collected from the Ohio River, July-August 1996. (+, presence [≤ 2%]; – , absence).

Algae	*A. plicata* (L)	*A. plicata* (H)	*Q. pustulosa* (L)	*Q. pustulosa* (H)
Chlorophyta				
Ankistrodesmus	–	–	+	–
Chlamydomonas	+	–	+	–
Chlorella	15.3 (8.7)	15.0 (11.2)	42.3 (18.8)	63.0 (29.4)
Chlorococcum	+	+	+	–
Closterium	–	–	+	–
Coelastrum	–	–	+	–
Cosmarium	–	–	+	–
Gonium	–	+	–	–
Mougeotia	+	+	+	–
Oedogonium	–	+	–	–
Oocystis	+	–	–	–
Pediastrum	–	+	–	–
Scenedesmus	6.2 (5.9)	5.2 (4.7)	6.6 (5.8)	–
Schroederia	+	–	–	–
Selenastrum	–	–	+	–
Spirogyra	+	–	–	–
Staurastrum	+	–	–	–
Bacillariophyta				
Achnanthes	+	–	+	–
Cocconeis	+	–	+	–
Coscinodiscus	+	+	+	–
Cyclotella	11.8 (2.7)	45.1 (11.1)	7.0 (3.8)	31.9 (30.8)
Cymbella	+	+	+	–
Diatoma	+	–	+	–
Fragilaria	–	–	+	–
Gomphonema	+	–	+	–
Melosira	5.7 (4.0)	16.0 (11.0)	8.8 (8.2)	2.8 (6.4)
Navicula	26.5 (7.4)	2.2 (0.6)	10.6 (6.2)	
Nitzschia	–	–	+	–
Pinnularia	+	+	+	–
Pleurosigma	–	–	+	–
Stephanodiscus	–	+	–	–
Surirella	+	–	–	–
Synedra	+	+	+	–
Tabellaria	+	–	–	–
Cyanoprokaryota				
Chroococcus	+	+	+	–
Merismopedia	–	+	–	–
Oscillatoria	+	–	+	–
Spirulina	–	–	+	–
Other				
Chromulina	–	+	–	–
Dinobryon	+	–	–	–
Peridinium	–	+	+	–
Chroomonas	+	–	–	–

found for intermediate-sized particles (5-30 µm). Maximum filtration rates for the unionid *Elliptio complanata* (Lightfoot, 1786) also were found for particles between 4 and 5 µm (Paterson, 1984). In our study, unionid gut analyses indicate that unionids ingest food particles between 4 and 80 µm in maximum dimension. Thus, zebra mussels and unionids in the Ohio River ingest food resources of similar size.

Relative abundances of algal genera ingested by zebra mussels and the two unionid species were very similar to those in water samples collected immediately above the mussel bed, giving no evidence of selective feeding. The only exception was the pennate diatom *Synedra* which was not readily ingested by unionids or zebra mussels,

Table 4. Percent relative abundances (SD) of algae in guts of *Dreissena polymorpha* and lightly (L) and heavily (H) infested *Amblema plicata* and *Quadrula pustulosa* collected from the Ohio River, July-August 1997. (+, presence [≤ 2%]; –, absence).

Algae	*A. plicata* (L)	*A. plicata* (H)	*Q. pustulosa* (L)	*Q. pustulosa* (H)	*D. polymorpha*
Chlorophyta					
Ankistrodesmus	–	–	+	–	–
Chlamydomonas	–	+	+	+	+
Chlorella	1.7 (1.4)	13.8 (10.1)	9.6 (8.8)	30.8 (24.7)	37.5 (16.8)
Chlorococcum	+	+	+	+	+
Cosmarium	–	–	+	–	–
Crucigenia	–	–	+	–	–
Gonium	–	–	+	–	–
Mougeotia	40.6 (7.5)	5.1 (7.0)	21.2 (11.7)	5.3 (9.3)	14.2 (12.2)
Oedogonium	+	–	–	–	–
Pandorina	+	–	+	–	–
Pediastrum	+	+	+	+	+
Scenedesmus	9.5 (3.6)	5.7 (2.0)	8.2 (5.9)	10.9 (9.6)	13.9 (10.7)
Trebouxia	+	–	–	–	–
Bacillariophyta					
Coscinodiscus	–	–	+	–	–
Cocconeis	–	–	+	–	–
Cyclotella	21.3 (11.9)	38.5 (18.6)	25.9 (6.9)	16.2 (12.7)	5.4 (4.5)
Diatoma	+	–	+	–	–
Gomphonema	+	–	–	–	–
Melosira	13.7 (9.2)	25.9 (16.7)	17.6 (9.4)	28.5 (18.3)	13.7 (10.4)
Navicula	+	+	+	–	+
Stephanodiscus	+	–	+	–	–
Synedra	–	–	+	–	–
Tabellaria	–	–	+	–	+
Cyanoprokaryota					
Aphanocapsa	–	–	+	–	–
Chroococcus	+	–	+	–	–
Oscillatoria	–	–	+	–	–
Other					
Peridinium	–	–	+	–	–

probably because of its cell length of > 100 µm. In unionid gut samples, *Mougeotia*, *Cyclotella*, and *Melosira* did appear in slightly greater abundance than in water samples. Regardless of selective feeding, unionid and zebra mussel gut contents contained a nearly identical assemblage of dominant algal genera. Thus, by ingesting food particles of similar size and type, zebra mussels in the Ohio River can compete directly with native unionids for food resources. However, competition can only be confirmed if the food items measured to assess diet overlap constitute a significant portion of the total diet of one of the potential competitors (Buss and Jackson, 1981). Unfortunately, there are no studies on the dietary or nutritional requirements of freshwater mussels.

Significant reductions in the mean AFDW and total algal cell number from gut samples of heavily infested versus lightly infested native freshwater mussels indicate that interference competition for food resources is occurring in the lower Ohio River. Since the arrival of the zebra mussel, unionid mortality thus far at various sites in the lower Ohio River has been estimated at 20-40% (P. Morrison, USFWS, pers. comm.). Interference with unionid feeding by zebra mussels, however, also could have long term consequences for the overall fitness of native mussels. Recent studies have shown that native unionids from the heavily infested Ohio River have significantly reduced glycogen levels relative to unionids from lightly infested areas (Patterson *et al.*, 1997). Glycogen is an important energy reserve for animals, especially bivalves (de Zwann and Zandee, 1972; Barber and Blake, 1981; Bayne and Newell, 1983; Haag *et al.*, 1993), and significant reductions can lead to chronic mortality or declines in reproductive success. Gonad development in marine bivalves, for example, has been shown to continue despite reduced energy reserves (Gabbott and Bayne, 1973; Bayne, 1975), but subsequent growth rates and energy reserves of the developing larvae decreased (Bayne, 1972; Helm *et al.*, 1973; Bayne *et al.*, 1975). Thus, by reducing food resources and interfering

Table 5. Percent relative abundances of algae at the surface and just above the mussel bed in the heavily (H) and lightly infested (L) Ohio River, July-August 1997. (+, presence [≤ 2%]; –, absence).

Algae	Surface (L)	Bottom (L)	Surface (H)	Bottom (H)
Chlorophyta				
Ankistrodesmus	–	+	–	–
Chlamydomonas	6	5	16	11
Chlorella	10	8	25	23
Chlorococcum	+	2	+	7
Gonium	–	+	–	–
Mougeotia	8	2	6	5
Oedogonium	+	+	–	+
Pediastrum	+	+	–	+
Scenedesmus	12	16	13	12
Staurastrum	+	+	+	–
Bacilariophyta				
Coscinodiscus	–	+	+	+
Cyclotella	4	5	3	13
Diatoma	+	+	–	+
Melosira	+	2	4	5
Navicula	–	+	–	+
Stephanodiscus	+	+	–	+
Synedra	12	43	11	10
Cyanoprokaryota				
Chroococcus	–	2	+	7
Merismopedia	8	7	–	–
Oscillatoria	+	6	3	3
Other				
Mallomonas	–	–	–	+

with normal feeding, zebra mussels could have their greatest effect on the long-term persistence of unionid beds in the lower Ohio River through reduction in reproductive success and recruitment.

ACKNOWLEDGMENTS

We thank Patty Morrison, Mitch Ellis, and others at the Ohio River Islands National Wildlife Refuge, as well as Dr. Andrew Miller and the United States Army Corps of Engineers for help in collecting mussels from the Ohio River. Thanks also go to Catherine Gatenby and the many volunteers who assisted with collection and processing of mussels in the field. Additionally, we thank Ashleigh Funk, Lana Shurts, and Doug Smith for laboratory assistance. This study was funded by Quick Response Funds of the Biological Resources Division, U. S. Geological Survey.

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Date of manuscript acceptance: 6 March 1998